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Influence of soil animals on nitrogen mineralisation in a northern Scots pine forest

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Summary :

An attempt was made to calculate the contribution by trophic groups of soil animals and microorganisms to net mineralisation of N in a Scots pine forest in Central Sweden. The analysis concerned the biologically most active part of the soil (0-30 cm depth) during a year. The analysis was based on estimates of biomass, respiration, C-fluxes and C:N-ratios of soil organisms and different food sources. It was assumed that soil organisms primarily use N for tissue production while excess N is excreted as ammonia or ammonium.

Total net mineralisation of N was calculated to be 28 kg ha^{-1} yr^{-1} according to a N-budget of the forest. Calculations of the contributions by trophic groups to this mineralisation were markedly affected by the choice of efficiency quotient for fluxes of C (for microorganisms) and assimilation efficiencies of N (for soil animals). According to the most probable alternative of calculation, soil animals were believed to mineralise/excrete about 30 % of the annual net mineralisation of N in the soil. Most of the animal mineralisation was effected by bacterivores, fungivores and carnivores, which all fed on N-rich food, whereas saprovores and herbivores, which fed on N-poor food, seemed to have little influence on N-mineralisation. The relatively high share of N-mineralisation of the soil animals was probably due to high C:N-ratios in litterfall and L-andF/H-layers, which meant that the microbial immobilisation/mineralisation balance was turned into a net immobilisation in the upper part of the soil.

Key words : bacteria, carbon, C:N-ratio, fungi, N-excretion, N-immobilisation, N-mineralisation, soil animals, trophic groups.

I. Introduction

Grazing of soil animals on microflora generally seems to stimulate nitrogen mineralisation in microcosm experiments (COLEMAN *et al.*, 1977; ANDERSON *et al.*, 1981). One interpretation might be that the grazing activity of microbial-feeding animals keeps down the microbial biomass and, thus, the microbial activity to immobilise N. It is also possible that the soil animals themselves exert an effect on N-mineralisation by excreting excess N when feeding on microorganisms rich in N (WOODS *et al.*, 1982).

In the present paper, I attempt to analyse the influence of different trophic groups of soil animals on N-mineralisation in a coniferous forest soil where N is a limiting element for plant growth. The analysis is based on field data of annual mean biomass and annual respiration (from PERSSON *et al.*, 1980), nitrogen flow (from, e.g., BRINGMARK, 1980), C:N-ratios in food substrates and organisms, and the hypothesis that soil organisms primarily utilise N for production (growth and reproduction), while excess N will be excreted, often as ammonia. The analysis concerns one year and most of the biologically active part of the soil (L, F/H and 0-30 cm mineral soil). All organisms were assumed to be in a steady state.

II. Site description

The study was performed at Ivantjärnsheden, Jädraås, in Central Sweden (lat. 60°49'N, long. 16°30'E, alt. 185 m above mean sea level). Long-term annual air temperature is 3.8° C and mean annual precipitation is about 600 mm. The study area had a regular stand of 120-year-old Scots pine (*Pinus sylvestris* L.), and its ground vegetation mainly consisted of *Calluna vulgaris* (L.) Hull, *Vaccinium vitis-idaea* L., *Pleurozium schreberi* (Brid.) Mitt. and *Cladonia* spp. An iron podsol has developed in the sandy soil. The humus form is a typical mor. The pH in water extracts is 4.0-4.6 in the upper soil layers. Litter (L) layer, humus (F/H) layer and 0-10, 10-20 and 20-30 cm mineral soil layers had a C:N-ratio of 49, 42, 35, 28 and 25 respectively (PERSSON *et al.*, 1980). A more detailed description of the site is given by PERSSON *et al.* (1980).

III. Methods

The present analysis was primarily based on data on annual mean biomass and annual respiration of soil organisms (Table I), which were estimated by PERSSON *et al.* (1980) as a result of samplings of soil organisms from July 1974 to June 1975. Nitrogen fluxes through the organisms and the resulting N-mineralisation were estimated according to the following steps of calculation :

1. C-fluxes were calculated from respiration data available from PERSSON *et al.* (1980) by means of different efficiency quotients for different trophic groups. The basic equations

$$C = P + R + F + U \quad \text{and} \quad C = A + F,$$

where C = consumption, P = production, R = respiration, F = defecation, U = excretion and A = assimilation (PETRUSEWICZ & MACFADYEN, 1970) give the relations between fluxes of matter and energy. For C-fluxes these quotients, P/C, R/C and F/C, were chosen to be 0.04, 0.16 and 0.80 for herbivores and saprovorous soil animals, 0.12, 0.18 and 0.70 for microbivores and 0.24, 0.56 and 0.20 for carnivores, respectively. For bacteria and fungi, P/A and R/A were chosen to be 0.2 and 0.8, respectively (see Discussion). Because all excretion was assumed to be in the form of NH_3 or NH_4^+ (see below), $U = 0$ in terms of carbon.

2. Data on C:N-ratios in bacteria, fungi, roots and dead organic matter were published elsewhere (see below). Such data on soil animals were lacking and, therefore, samples of litter and humus layers were taken in the 120-year-old Scots pine stand. The animals were extracted in Tullgren funnels into jars with moistened plaster of Paris. Live specimens were classified, removed to empty glass tubes, killed by freezing at -20° C and dried for 24 hours at + 60° C in a vacuum drier. Samples contained a minimum of 1 mg d.wt., and the animals were homogenised before being analysed in a Carlo-Erba Elemental Analyser 1106 at the Department of Chemistry, Swedish University of Agricultural Sciences.

3. A N-budget was constructed based on data available from previous studies of atmospheric deposition and leaching (BRINGMARK, 1980), biological N-fixation (GRANHALL & LINDBERG, 1980), litterfall (FLOWER-ELLIS & OLSSON, 1978; PERSSON *et al.*, 1980), root litter formation (PERSSON, 1980), C:N-ratios in litter fractions (BERG & STAAF, 1981) and increment in plant biomass (ANDERSSON *et al.*, 1980) according to the N-flow structure in Fig. 1. Apart from dead organic matter, all compartments in Fig. 1 were assumed to be in a steady state. Root uptake of N, including N translocated from the mycorrhiza, was calculated as the sum of above- and below-ground litter production and increment in plant biomass minus atmospheric deposition in the canopy. N-uptake for mycorrhizal growth was calculated assuming the same C:N-ratio and the same turnover rate as for saprotrophic fungi. From these estimates, total N-mineralisation was calculated as a difference.

4. The flows of N in animal consumption and production were estimated from the C-fluxes (see **1.**) and C:N-ratios (see **2.**), assuming that P_C:P_N (C in production : N in production) and C_C:C_N were equal to the C:N-ratios in the appropriate organisms and foods, respectively. No data were available on N-assimilation from animal guts and the resulting effect of N-concentration in faeces. Therefore, three alternatives (A, B and C) were analysed. Alternative A assumed that C and N were assimilated in proportion to the concentrations in the consumed food, *i.e.*, that C:N in faeces was equal to that in food. Alternative B assumed that N-uptake from the guts was more efficient, leading to a C:N in faeces that was 1.33 times that in food. Alternative C assumed that C:N in faeces was twice that in food.

5. Excess N, that was not defecated or used for production of cells, was considered to be excreted.

6. Saprotrophic bacteria, fungi and soil animals were assumed to assimilate/consume dead organic matter. Because the C-fluxes were determined as in **1.**, and the N-fluxes had to balance all inflows of N to «dead organic matter» in Fig. 1, different C:N-ratios were assimilated/consumed by the saprotrophic organisms as a result of alternatives A-C, that also caused different values of N in faeces and dead bodies.

IV. Results

Basic data on annual mean biomass and annual respiration (from PERSSON *et al.*, 1980) and estimates of C-fluxes are given in Table I. These data, irrespective of their accuracy, were used in the following analysis.

TABLE I

Annual mean biomass and annual fluxes of carbon in consumption (*C*), assimilation (*A*), production not used for predation (P_{np}), production used for predation (P_p), respiration (*R*) and defecation (*F*) in the litter and soil layers to a depth of 30 cm at Ivantjärnsheden during 1974-75. (Partly from PERSSON *et al.*, 1980).

	Biomass	**C-flux (g C m^{-2} yr^{-1})**					
	(g d.wt. m^{-2})	*C*	*A*	P_{np}	P_p	*R*	*F*
Bacteria	39	-	149	7.1	23	119	-
Fungi	121	-	125	12	13	100	-
Mycorrhizal fungi	34	-	35	3.4	3.6[a]	28	-
Saprotrophic fungi	87	-	90	8.7	9.2[a]	72	-
Soils animals	1.7	-	-	3.1	2.1	9.4	34
Saprovores	0.24	11	2.2	0.1	0.4[b]	1.7	8.7
Bacterivores	0.37	23	6.8	2.1	0.6[b]	4.1	16
Fungivores	0.70	13	3.8	0.4	1.1[b]	2.3	9.0
Carnivores	0.41	2.1	1.7	0.5	0	1.2	0.4
Herbivores	0.007	0.33	0.06	0.003	0.01[b]	0.05	0.27
Total	161	-	-	22	-	228	34

[a] Selection for grazing by fungivores assumed to be proportional to biomass.

[b] Selection for predation by carnivores assumed to be proportional to biomass.

The chemical analyses indicated that most soil animals had a C-concentration of 50-55 % and a N-concentration of 8-12 % (Table II). The diplopods were exceptions, probably due to high concentration of $CaCO_3$ in the exoskeleton. This limited set of data did not indicate any clear differences in N-concentrations between trophic groups of soil animals. Because the diplopods had a very low biomass and, thus, did not affect the total results, it seemed justified to use 50 % as the C-concentration and 10 % as the N-concentration for all trophic groups of soil animals.

TABLE II

Carbon and nitrogen concentrations (% of d.wt.) in soil animals at Ivantjärnsheden (mean of at least two analyses).

	Sampling period	C	N
Nematoda	May 1979	52.5	11.5
Enchytraeidae (*Cognettia sphagnetorum)*	Oct. 1978	50.9	10.8
Collembola (mainly *Isotoma* spp.)	Oct. 1978	52.4	11.8
Diplopoda (*Proteroiulus fuscus)*	May 1979	35.8	4.8
Elateridae larvae	Oct. 1978	53.2	11.0
Cantharidae larvae	Oct. 1978	55.3	9.5
Formicidae (*Myrmica ruginodis)*	Oct. 1978	56.0	9.2
Gamasina (*Pergamasus* and *Veigaia* spp.)	Oct. 1978	52.2	11.1
Cryptostigmata adults	Oct. 1978	47.3	8.9
Araneae	Oct. 1978	53.3	10.6

According to BÅÅTH & SÖDERSTRÖM (1979), fungi at Ivantjärnsheden had C- and N-concentrations of 45 and 3.7 %, respectively, and these percentages were used here for both saprotrophic and mycorrhizal fungi. The corresponding figures for bacteria were assumed to be 48 and 4.0 % (CLARHOLM, pers. comm.). Fine roots usually had C:N-ratios close to 100 (BRINGMARK *et al.*, unpubl. data), but since the analyses probably included woody tissues, the herbivore food was assumed to have a C:N-ratio of 50. Saprotrophic fungi, bacteria and soil animals assimilated/consumed dead organic matter that had decreasing C:N-ratios with increasing depth in the soil, 51, 47 and 36 in the L-layer, F/H-layer and the 0-10 cm mineral soil layer, respectively.

According to the percentages in soil organisms given above and the biomass estimates in Table I, the mean amounts of N bound in soil organisms were 32 kg ha^{-1} in saprotrophic fungi, 13 in mycorrhizal fungi, 16 in bacteria and 1.7 in soil animals (Fig. 1), *i.e.*, a total of 62 kg N ha^{-1} in soil organisms. Total N bound in dead organic matter was 1070 kg ha^{-1} (PERSSON *et al.*, 1980) and the mean pool of inorganic N (NH_4^+-N and NO_3^--N) in the soil solutions was 1.6 kg ha^{-1} (in 1976) (POPOVIĆ, 1980).

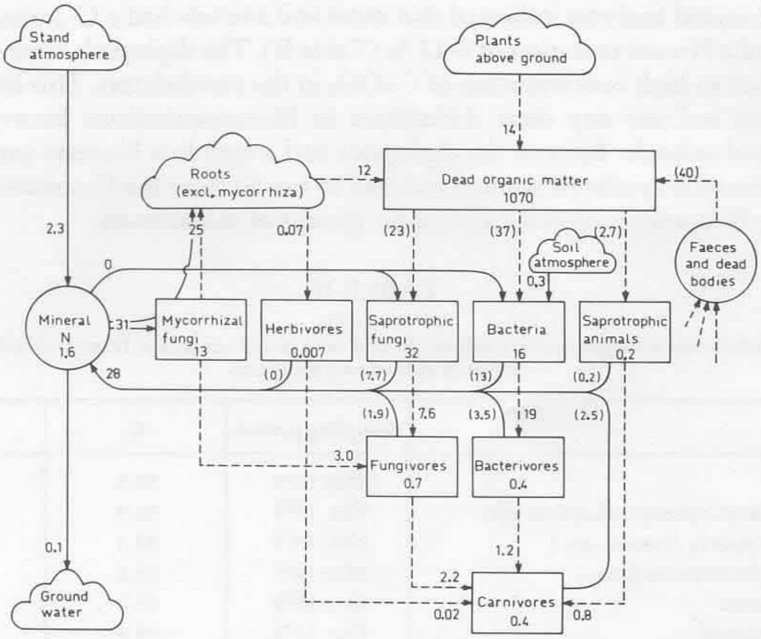

Figure 1 Nitrogen flow diagramme in the soil in the 120-year-old Scots pine stand at Ivantjärnsheden to a depth of 30 cm in the mineral soil. Boxes denote annual means of N (kg ha^{-1}) in organisms, dead organic matter and soil solution. Solid lines ending in an arrow denote fluxes (kg N ha^{-1} yr^{-1}) of inorganic nitrogen. Broken lines denote fluxes of organic nitrogen. Fluxes of faeces and dead bodies are only incompletely depicted. Values within parentheses are affected by the way of calculation and refer to alternative B (see text). Estimates of net mineralisation (28) and net immobilisation (0) are given instead of total mineralisation and total immobilisation that were not estimated.

TABLE III

Nitrogen budget for the joint L, F/H and 0-30 cm mineral soil layers at Ivantjärnsheden.

	kg N ha^{-1} yr^{-1}	Data source
Inorg. N in throughfall	2.3	1
Biological N-fixation	0.3	2
Litterfall	14.2	3,4,5
Root litter formation	11.8	4,5,6
Total input to soil	28.5	
Leaching	0.1	1
Uptake by roots	25.0	1,3,4,5,6,7
Total loss from soil	25.1	
Accumulation in dead org. matter	3.4	

[1]BRINGMARK (1980), [2]GRANHALL & LINDBERG (1980), [3]FLOWER-ELLIS & OLSSON (1978), [4] PERSSON *et al.* (1980), [5] BERG & STAAF (1981), [6] PERSSON (1980), [7] ANDERSSON *et al.* (1980).

The N-flux balance available from previous studies indicated an accumulation of 3.4 kg N ha^{-1} yr^{-1} in dead organic matter (Table III). N-uptake for production of mycorrhizal fungi was calculated to be 5.8 kg N ha^{-1} yr^{-1}. Because the uptake by higher plants was 25 kg N ha^{-1} yr^{-1} (Table III), the net uptake from the soil solution was about 31 kg N ha^{-1} yr^{-1} (Fig. 1) and the corresponding supply through mineralisation about 28 kg N ha^{-1} yr^{-1} (Fig. 1).

Estimates of net N-mineralisation by different trophic groups are shown in Table IV. The contribution by soil animals to the total net N-mineralisation was estimated to be 10, 29 and 49 % according to the alternatives A,B and C, respectively. The different alternatives of calculation also affected the estimates of assimilation/consumption of N by saprotrophic organisms and the estimates of N in faeces (Table IV). In all alternatives the total production of dead bodies was estimated to be 22 kg N ha^{-1} yr^{-1}, which meant that the reflux of N in dead bodies and faeces to dead organic matter (40 kg ha^{-1} yr^{-1} in alternative B) was much higher than the corresponding input in litter fractions (see Fig. 1).

TABLE IV

Net N-mineralisation (kg ha^{-1} yr^{-1}) by different soil organism groups. A, B and C are different alternatives, where assimilation of N from the animal guts is successively more efficient (see text). Effects of the alternatives on other fluxes of N are also shown (*cf.* Fig. 1).

	A	B	C
Bacteria	16.0	12.5	8.9
Saprotrophic fungi	9.8	7.7	5.6
Soil animals	2.7	8.2	14.0
Saprovores	0	0.2	0.6
Bacterivores	0.2	3.5	6.9
Fungivores	0.1	1.9	3.8
Carnivores	2.3	2.5	2.8
Herbivores	0	0	0.01
Total	28	28	28
Assimilation by saprotrophic fungi	25	23	20
Assimilation by saprotrophic bacteria	41	37	34
Consumption by saprotrophic animals	3.0	2.7	2.5
Defecation plus non-predatory death	46	40	34

V. Discussion

The analysis showed that two factors affected the estimates of N-fluxes markedly : (1) the choice of efficiency quotients for C-fluxes and (2) the assimilation efficiencies of N for soil animals.

Most organism groups in Fig. 1 feed on or assimilate resources that have much lower N-concentrations than in the organisms themselves. Low *P*/*R*-ratio is one means of getting sufficient concentration of N in the cells. HEAL & MACLEAN (1975) suggested a *P*/*R* of 0.4:0.6 for the microflora and saprovorous soil animals and this was also adopted by PERSSON *et al.* (1980). According to (6) in Methods, this ratio implied that the saprotrophic organisms should assimilate/consume a C:N-ratio of 20-25 to excrete appropriate amounts of mineral N. Since the upper part of the soil had much higher C:N-ratios in the dead organic matter (see above), a *P*/*R* of 0.2:0.8 was chosen for these groups (see Methods). Such a low production efficiency differs from that found in laboratory cultures (e.g., HEAL & MACLEAN, 1975; McGILL *et al.*, 1981), but in the long-term field situation reassimilation by microorganisms of dead microorganisms might be essential, resulting in a low *P*/*R*-ratio for the microorganisms as a whole. The saprotrophic animals at Ivantjärnsheden mainly consisted of the enchytraeid *Cognettia sphagnetorum* (Vejd.). This species has a very low production efficiency according to STANDEN (1973), and a *P*/*R* of 0.2:0.8, therefore, seemed to be appropriate also for the saprotrophic animals.

Different values of assimilation efficiency of N from animal guts resulted in different rates of N-mineralisation. Inefficient N-uptake by the animals (alternative A) meant that the animals could only excrete small amounts of mineral N (Table IV). Efficient N-uptake (alternative C) led to high excretion rates. In alt. A, the saprotrophic organisms needed an average C:N-ratio of 36 in the substrate assimilated/consumed, while the ratios needed were 40 in alternative B and 44 in alternative C. Most organism activity occurred in the L, F/H and 0-10 cm mineral soil layers, where the average C:N-ratio was 40 in the dead organic matter. Thus, alternative B, with a microbial need of N corresponding to a C:N-ratio of 40, fits this situation.

Different trophic groups of soil animals were estimated to have different contributions to net N-excretion depending on alternatives A-C. In all alternatives, carnivores were estimated to excrete a significant amount of N (Table IV) despite a low biomass (Table I). This was primarily due to the high N-quality of the food. According to alternatives B and C, bacterivores were the most important of the soil animals in excreting N. The ability of microbial-feeding protozoans and nematodes to increase rates of N-mineralisation is in good agreement with microcosm experiments (e.g., COLEMAN *et al.*, 1977; WOODS *et al.*, 1982). The fungivore influence on N-mineralisation is more difficult to evaluate. The present data in Table IV indicate a significant contribution in alternatives B and C, but it is possible that animals classified as pure fungivores partly feed on dead organic matter, which will reduce the excretion of N. Finally, saprovorous and herbivorous soil animals seem to have very little influence on N-mineralisation (Table IV) because nearly all N available will be used for growth.

A closer analysis of the different soil layers indicated that the microflora had a net immobilisation in the upper parts of the soil. BRINGMARK (1980) found a decrease in mineral N from 2.3 to 1.2 kg ha^{-1} yr^{-1} between the inflow to and outflow from the L-layer at Ivantjärnsheden. Because no roots occurred in that layer and soil animals can not immobilise mineral N, the immobilisation by the microflora must have been even higher than the lacking 1.1 kg ha^{-1} yr^{-1}. In the F/H-layer, root litter of C:N = 90 - 100 was added to the soil, and it is probable that the microbial mineralisation of N was also low in this layer. At greater depths, where the C:N-ratio was ~~higher~~, the microbial immobilisation/mineralisation balance was probably turned into a net mineralisation.

A part of the animal excretion of N might be release of excretory products other than ammonia, for example, urea, uric acid and allantoin (COCHRAN, 1975). The present knowledge indicates that ammonia is the main product for aquatic life forms, such as protozoans and nematodes, while terrestrial forms excrete materials less dependent on water elimination. However, recent studies indicate that ammonia is also a common excretory product of terrestrial forms (see COCHRAN, 1975), and in lack of appropriate studies of excretory products of soils animals, I considered all excreted N as mineral N in this analysis.

In conclusion, the present study indicated that the soil animals at Ivantjärnsheden with a low biomass (1 % of total soil heterotrophs) and relatively low respiration (4 % of heterotrophic soil respiration) might have a significant excretion of N. The choice of assimilation efficiency of N from animal guts turned out to be critical for the estimates of N-mineralisation. It is essential to determine this efficiency in order to make the estimates more accurate, and such studies have also been started at our laboratory for selected types of food and soil animals.

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